Limulus Vision in the Marine Environment

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Abstract. Horseshoe crabs use vision to find mates. They can reliably detect objects resembling potential mates under a variety of lighting conditions. To understand how they achieve this remarkable performance, we constructed a cell-based realistic model of the lateral eye to compute the ensembles of optic nerve activity ("neural images") it transmits to the brain. The neural images reveal a robust encoding of mate-like objects that move underwater during the day. The neural images are much less clear at night, even though the eyes undergo large circadian increases of sensitivity that nearly compensate for the millionfold decrease in underwater lighting after sundown. At night the neural images are noisy, dominated by bursts of nerve impulses from random photon events that occur at low nighttime levels of illumination. Deciphering the eye's input to the brain begins at the first synaptic level with lowpass temporal and spatial filtering. Both neural filtering mechanisms improve the signal-to-noise properties of the eye's input, yielding clearer neural images of potential mates, especially at night. Insights about visual processing by the relatively simple visual system of *Limulus* may aid in the design of robotic sensors for the marine environment.

Introduction

The world is rich with sensory information, and animals are highly efficient at extracting what is essential for their survival. The retina begins the processing of visual infor-

mation by transforming patterns of incident light intensity into trains of impulses in optic nerve fibers (Dowling, 1987). The retina encodes information it receives in a reliable and efficient manner (Rieke *et al.*, 1997) but does not encode all of it. Rather, the retina extracts certain features in the visual scene at the expense of others (Lettvin *et al.*, 1959). An important first step for exploring the neural code the eye transmits to the brain when an animal sees is to understand what an animal can see in its natural habitat. The next step is to examine the retinal coding of natural scenes in activity of optic nerve fibers. Recordings from single nerve fibers have indeed yielded useful insights about retinal function; however, it is difficult to infer from them the information transmitted by arrays of optic nerve fibers to the brain about the complex patterns of illumination animals encounter in their natural habitat. Techniques such as multi-electrode arrays (Meister *et al.*, 1994) and voltage-sensitive dyes (Wong *et al.*, 1995) can access patterns of activity generated by ensembles of retinal neurons, but they are not practical for recording from large numbers of optic nerve fibers in behaving animals.

A Computational Model of the *Limulus* Eye

An alternative approach is to construct a realistic computational model of the eye. The relative simplicity of the eyes of lower vertebrates and invertebrates offers the best opportunities (Werblin, 1991; Teeters *et al.*, 1997). The lateral eye of the horseshoe crab *Limulus polyphemus* is a particularly attractive model system for the following reasons: first, its visually guided behavior is well known (Barlow *et al.*, 1982; Powers *et al.*, 1991; Herzog *et al.*, 1996); second, it processes visual information with integrative mechanisms shared by more complex systems (Barlow, 1969; Ratliff, 1974); and third, its lateral eye contains the largest neural network (~1000 neurons) for which a quantitative cell-based model exists (Hartline and Ratliff, 1957, 1958; Barlow and Quarles, 1975; Barlow *et al.*, 1993b).

Figure 1. A horseshoe crab, *Limulus polyphemus*, mounted with a video camera, "CrabCam," for recording underwater movies and a microsuction electrode for recording responses from a single optic nerve fiber. A white Teflon cap (2.5 cm diameter) seals the recording chamber, which is attached to the carapace anterior to the right lateral eye. The barrel of the microsuction electrode protrudes from the recording chamber to the right. Tethers lead the video and optic nerve signals to recording electronics located on shore or in an overhead skiff as the animal moves about underwater at depths of 0.5 to 1 m. Experiments were carried out in an estuary near the Marine Biological Laboratory, Woods Hole, Massachusetts.

We have constructed a computational model of the lateral eye that predicts optic nerve responses with good accuracy (Passaglia *et al.*, 1998). In brief, the model treats the retina as an array of neurons that samples visual space as the compound eye does, incorporates the known excitatory and inhibitory integrative mechanisms of the retina, and adapts to changes in ambient illumination.

Our strategy for examining the retinal code underlying behavior is to first videotape the lateral eye's view of its underwater world with an animal-mounted camera ("CrabCam") while simultaneously recording from a single optic nerve fiber of an ommatidium viewing the central region of the videotaped scene (Passaglia *et al.*, 1997a). Figure 1 shows the CrabCam and the watertight recording chamber mounted on an animal before it enters the water and passes near submerged mate-like objects near the water's edge in Woods Hole, Massachusetts. Back in the laboratory we digitize the CrabCam recordings and feed them to the cell-based model, which then computes the arrays of optic nerve activities in response to the underwater scenes. The computed arrays of activities are converted to a grey scale and mapped to their appropriate retinal location, generating "neural images" of the eye's input to the brain (Fig. 2). Finally, we assess the accuracy of the model's predictions by comparing the response recorded from a single optic nerve fiber to that computed by the model for the corresponding receptor. Correlation coefficients between recorded and com-

Figure 2. Computed responses of the *Limulus* eye and brain to moving mate-like objects day and night. Top panel shows the results for a low-contrast object, and the bottom panel shows those for a high-contrast object. The two objects approximate the size (0.3 m diameter, 0.15 m high) and range of contrasts of adult female crabs. They move across the visual field at a distance of 0.6 m, where most visual detection occurs (Herzog *et al.*, 1996). The left column ("Visual stimulus") shows CrabCam images of the high- and low-contrast objects after sampling by the eye's optical apparatus. The arrays of pixels indicate the light intensities incident on the 16 × 16 array of ommatidia viewing the videotaped scene. The adjacent column ("Neural image") shows the ensembles of optic nerve activities computed by the retinal model in response to the visual stimuli on the left. The arrays of pixels in the neural images give the computed firing rates of optic nerve fibers mapped onto a gray scale with black set to 0 impulses/s and white set to twice the mean firing rate. Photon fluxes were reduced by $\sim 10^6$ in the model calculations to simulate the "Night" state of the eye. The neural images represent snapshots of the responses of the 16 × 16 array of ommatidia to the visual stimulus. The third column shows the computed neural images of synaptic activity in the brain after "temporal integration" of the retinal neural image with an integration time of 400 ms. The synaptic activities are mapped onto a gray scale with black set to 0 mv and white set to twice the mean amplitude of the synaptic potential. The fourth column displays the computed neural images of synaptic activity in the brain after "spatial summation" within the excitatory centers of the presumptive receptive fields of laminar cells. Note that at night, phototransduction noise obscures the neural images of the visual stimuli, but temporal and spatial integration partially recovers them.

puted responses are typically greater than 95% ($n = 5$) under controlled laboratory conditions but lower for field experiments because of the difficulty of precisely determining the stimulus to the recorded ommatidium. Once satisfied with the accuracy of the model's predictions, we analyze the neural images for information the eye sends to the brain when the animal sees.

The *Limulus* Eye Functions as a Global Feature Detector

The eye transmits to the brain robust "neural images" of objects having the size, contrast, and motion of potential mates (Passaglia *et al.*, 1997a). Inspection of the neural images computed for the daytime state of the eye in Figure 2 shows that the eye is highly sensitive to images of crab-
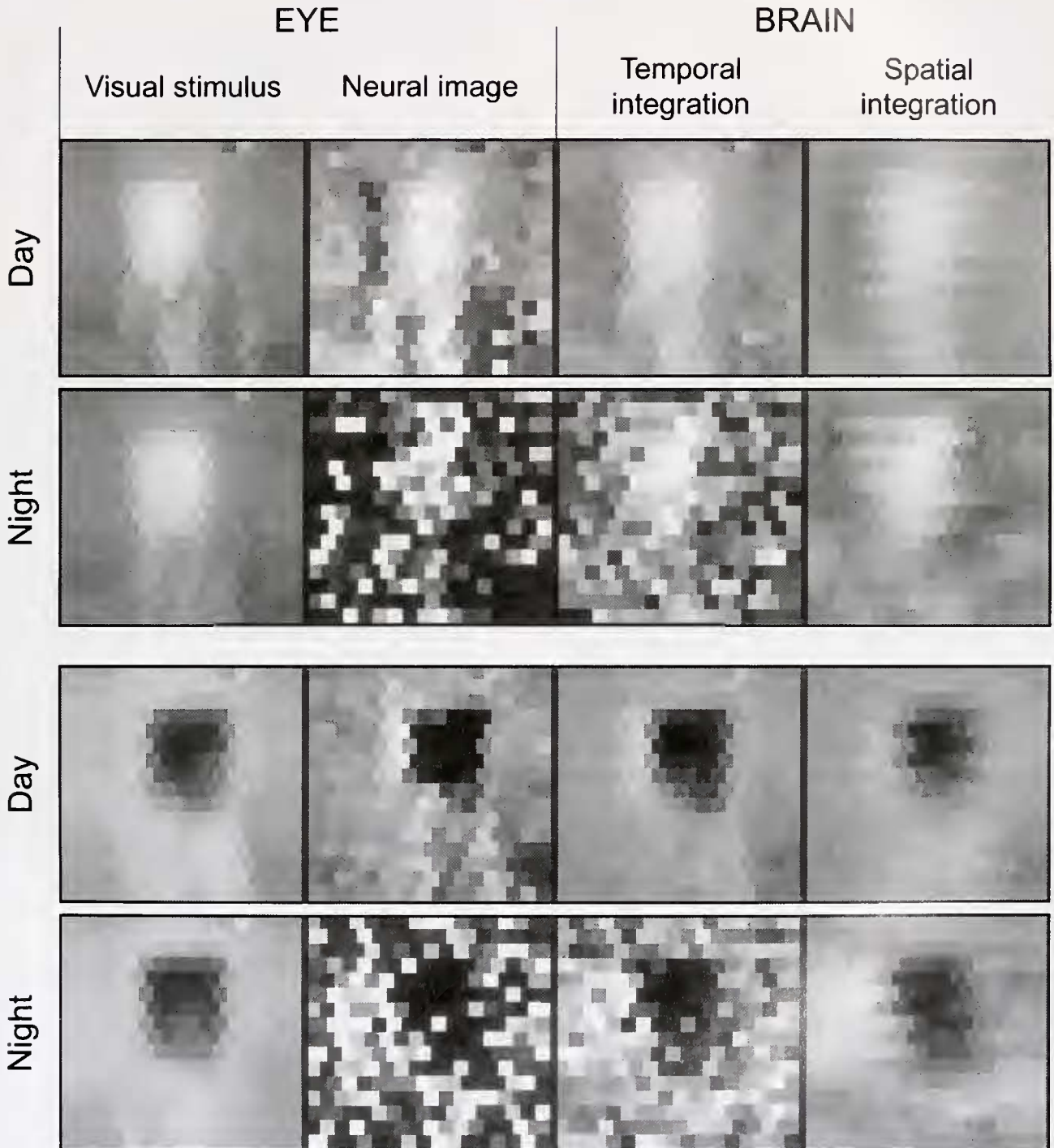
Table 1

Circadian rhythms in the Limulus *lateral eye*

Retinal property	Day	Night	Reference
Efferent input	Absent	Present	Barlow *et al.*, 1977; Barlow, 1983
Gain	Low	High	Renninger *et al.*, 1984; Barlow *et al.*, 1987
Noise	High	Low	Barlow *et al.*, 1977; Kaplan and Barlow, 1980; Barlow *et al.*, 1993a
Quantum bumps	Short	Long	Kaplan *et al.*, 1990
Frequency response	Fast	Slow	Batra and Barlow, 1990
Dark adaptation	Fast	Slow	Kass and Berent, 1988
Lateral inhibition	Strong	Weak	Renninger and Barlow, 1979; Ruta *et al.*, 1999
Cell position	Proximal	Distal	Barlow and Chamberlain, 1980; Barlow *et al.*, 1980
Pigment granules	Clustered	Dispersed	Barlow and Chamberlain, 1980
Aperture	Constricted	Dilated	Chamberlain and Barlow, 1977, 1987
Acceptance angle	6°	13°	Barlow *et al.*, 1980
Photomechanical movements	Trigger	Prime	Chamberlain and Barlow, 1987
Photon catch	Low	High	Barlow *et al.*, 1980
Membrane shedding	Trigger	Prime	Chamberlain and Barlow, 1979, 1984
Arrestin mRNA level	High	Low	Battelle *et al.*, 2000
Intense light effects	Protected	Labile	Barlow *et al.*, 1989
Visual sensitivity	Low	High	Powers and Barlow, 1985; Herzog *et al.*, 1996

size objects moving within the animal's visual range at about the speed of a horseshoe crab (15 cm/s). Indeed, measurements of the spatial and temporal transfer functions of the eye using linear systems analysis show that it functions as a tuned spatiotemporal filter. These filtering properties can readily account for the animal's ability to see high-contrast objects but not low-contrast ones. Natural fluctuations of underwater lighting enhance the visibility of low-contrast objects. Beams of light created by overhead waves strobe the underwater scene in a range of frequencies (~2–6 Hz) for which the temporal transfer function shows the eye is maximally sensitive. Such wave-induced flicker increases the visibility of low-contrast, crab-sized objects during the day, as observed in field studies (Passaglia *et al.*, 1997b; Krutky *et al.*, 2000). The strobic light evokes coherent bursts of nerve impulses from clusters of neighboring ommatidia as the object moves across the visual field. These coherent bursts of activity are equal in amplitude to those evoked by moving, high-contrast objects, which is consistent with the animal's ability to detect mate-like objects regardless of their contrast. Stationary objects, either high or low contrast, are hardly recognizable in the computed neural images (not shown).

Limulus vision requires both stimulus motion and activities generated over ensembles of retinal receptors. The neural code for moving crab-like objects is not found in ambiguous messages of individual optic nerve fibers but in the coherent activity of small ensembles of nerve fibers. Such "distributed coding" has been detected in amphibian (Warland *et al.*, 1997; Brivanlou *et al.*, 1998) and mammalian visual systems (Field, 1994; Alonso *et al.*, 1996; Berry *et al.*, 1997; De Vries, 1999; Meister and Berry, 1999). In *Limulus*, stimulus motion binds these coherent activities

together, sending a robust signal to the brain about potential mates. Endowed with spatiotemporal filtering properties, the eye is a sensitive detector of moving, crab-sized objects.

A Circadian Clock Modulates Lateral Eye Sensitivity

The *Limulus* eye operates in two distinct states: daytime and nighttime. It not only responds to changes in illumination, it anticipates them. At dusk a circadian oscillator in the brain transmits efferent optic-nerve signals to the lateral eye, influencing almost every physiological and anatomical property of the retina (Table 1).

The endogenous rhythms of the retina combine with mechanisms of light and dark adaptation to increase visual sensitivity by about 10^6 at night, nearly compensating for the decrease in the intensity of illumination in the animal's marine environment. In our initial theoretical analysis of retinal coding discussed above, we constructed a computational model to simulate the daytime state of the eye. To examine the retinal coding that underlies vision at night, we must modify our computational model so that it can account for the circadian changes in lateral eye function. We have developed a "nighttime" model that includes most of the circadian changes listed in Table 1.

Photon Noise Dominates Retinal Responses at Night

Neural images of mate-like objects are less clear at night. They are dominated by bursts of spikes triggered by random photon events that characterize low nighttime levels of illumination (Hitt *et al.*, 2000). The high-contrast object is detectable in the computed neural image in Figure 2, but the low-contrast object is almost completely obscured by random photon events. Computations require the setting of
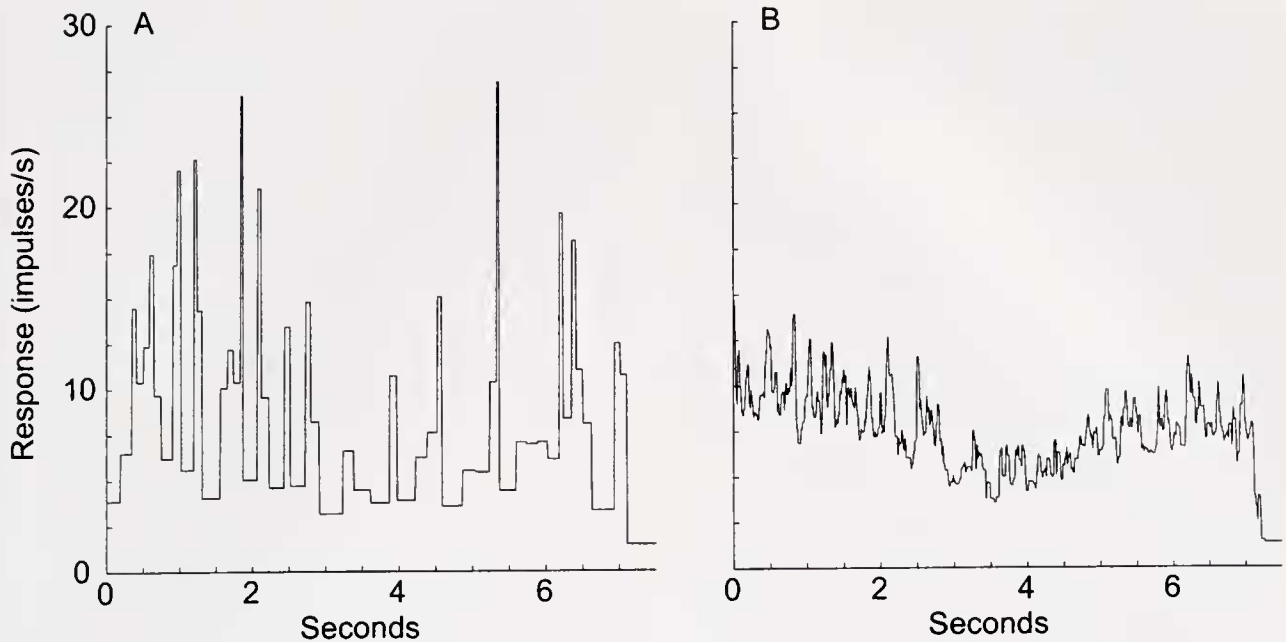
Figure 3. (A) Response of a single optic nerve fiber to a black mate-like object moving across the visual field. Plotted are the instantaneous frequencies, reciprocals of the intervals between nerve impulses, of the train of spikes over a 7-s period. The highly variable discharge reflects phototransduction noise caused by random photon events at low nighttime light levels. (B) Average of the responses of the single optic nerve fiber to 15 repetitions of the visual stimulus. Modulation by the moving black object is evident in the average response but not in the single one.

initial conditions, and an important initial condition is the mean light level of the visual scene. To simulate the nighttime state we reduce the mean light level by 10^6 relative to daytime levels. At such low light levels the Poisson nature of photon absorption events produces substantial phototransduction noise that can obscure signals generated by visual stimuli.

The response of a single optic nerve fiber in Figure 3A recorded under nighttime light levels is indeed variable. It shows no clear sign that a high-contrast crab-sized object had moved across the visual field. This experiment was performed in the laboratory because the Crabcam is insensitive to the low light levels in the animal's habitat at night. To overcome this problem we simulated nighttime conditions by aligning an animal in front of a monitor that played back CrabCam recordings made in the animal's habitat. The output of the monitor was attenuated by 10^6 with neutral density filters to approximate nighttime levels of illumination. The highly variable optic nerve response shown in Figure 3A is consistent with the noisy neural images in Figure 2 that were computed with the nighttime model of the eye.

Brain Processing Enhances Retinal Signals

How does the brain extract a reliable signal from such a noisy retinal input? Optic nerve fibers carrying the retinal

signals synapse on neurons of the lamina of the brain. Single-cell recordings show that the laminar synapses integrate retinal signals with a time constant of about 400 ms (Passaglia *et al.*, 1997a). To assess the effect of these "slow" synapses we added a stage of temporal integration to the computational models. Figure 2 shows that synaptic integration with such a long time constant suppresses the high-frequency fluctuations in optic nerve activity both day and night. The effect is especially striking in the neural images computed for the daytime state where temporal integration nearly recovers the visual stimulus. It is interesting that in another invertebrate visual system, that of the fly *Lucilia cuprina*, temporal integration reliably recovered the stimulus-induced response component from noisy neuronal signals in the motion pathway (Warzecha and Egelhaaf, 1997). Returning to *Limulus*, temporal integration of the neural images generated by the retina in its nighttime state does not recover the visual stimulus. The burstiness evoked by random photon events (Fig. 2) remains prominent and obscures information about the visual stimulus.

Because horseshoe crabs can see potential mates nearly as well at night as during the day, the brain must possess additional neural mechanisms for processing the retinal input, although these mechanisms need not be located in the lamina. One such mechanism could be spatial integration within the receptive fields of laminar neurons (Hitt *et al.*,

2000). Although the dimensions of receptive fields in the lamina have not been mapped with precision, we assumed for preliminary calculations that each laminar neuron sums optic nerve inputs from a 3×3 matrix of retinal receptors. Figure 2 shows that adding such a stage of spatial integration significantly improves the signal-to-noise properties of the neural images in the brain computed for the nighttime state of the eye. Integrating the optic nerve responses from an array of retinal receptors viewing partially overlapping regions of visual space is nearly equivalent to averaging the responses from a single receptor. Indeed, Figure 3B shows that averaging responses of a single receptor to repeated visual stimuli yielded a clear modulation of optic nerve activity, whereas a single response exhibited no detectable modulation. We conclude that circadian increases in the sensitivity of the lateral eye in combination with lowpass spatial and temporal filtering in the brain can yield detectable visual signals in the presence of high phototransduction noise caused by low nighttime light levels. The circadian and neural integrative mechanisms may help explain how *Limulus* can see so well at night.

What Is the Neural Basis of Behavior?

How does the intricate circuitry of a nervous system receive sensory information, process it, and generate a behavioral response? Analyzing a relatively simple nervous system may yield important insights about the functioning of more complex ones. Indeed the visual system of *Limulus* has proven complex enough to be interesting, yet simple enough to be understood. Using a computational approach, we unraveled its coding properties and determined the neural image it sends to the brain about behaviorally relevant stimuli during the day. The *Limulus* eye, however, turned out not to be so "simple" after all. A circadian clock increases its sensitivity at night, enabling the animal to detect potential mates, a critical task that it performs equally well day and night. The clock does so by modulating almost every property of the retina, from stabilizing rhodopsin to weakening lateral inhibition and increasing photoreceptor gain (see Table 1). The challenge addressed in this paper is to understand how the eye efficiently encodes information about potential mates under the photon-limited conditions of the animal's marine environment at night. The answer in part appears to be that coding mechanisms in the eye together with integrative mechanisms in the brain overcome environmental noise to enhance the neural images of behaviorally important visual stimuli.

The neural basis of visually guided behavior has been studied extensively in another invertebrate, the fly. Particular attention has been paid to understanding how the fly visual system adapts to, encodes, and processes natural stimuli (Review: Rieke *et al.*, 1997). Adaptative mechanisms in the fly retina appear to enhance the efficiency of

coding information about natural scenes (Review: Laughlin, 1994). In more central pathways, adaptive motion-sensitive mechanisms rescale the dynamic range of neural responses to match that of stimuli and thereby maximize information transmission (Brenner *et al.*, 2000). Adaptation of the motion-sensitive mechanisms decreases contrast sensitivity while preventing saturation of neural responses and preserving receptive field response properties (Harris *et al.*, 2000). Whether *Limulus* possesses such adaptive mechanisms is not known. However, as described above, retinal mechanisms endow the *Limulus* eye with high sensitivity to the motion of natural stimuli, and central mechanisms suppress noisy retinal signals to recover stimulus-induced responses.

This brings us to more complex systems such as the vertebrate retina. With tens of millions of cells, dendritic processes, and synaptic contacts, the task of deciphering its neural code is indeed daunting. Developing a cell-based, realistic computational model as we did for *Limulus* appears unrealistic. A different computational approach is needed; one that by necessity models ensembles of neurons. The danger is that such modeling may overlook essential details in the neural circuitry. As was the case for *Limulus*, important insights can come from understanding the function of a sensory organ and how it adapts to changing environmental conditions. Endogenous adaptation mechanisms, such as efferent inputs and circadian oscillators, can often reveal critical aspects of underlying neural mechanisms. Perhaps most important of all is first to understand the role of a sensory modality in an animal's life and then to investigate the underlying neural mechanisms.

Implications for Artificial Sensory Systems

Sensory systems, especially those of invertebrates, often serve primary functions. They are highly efficient at extracting from the physical world specific information for behaviors essential for survival: mating, finding food, and avoiding predators. In some animals, subsections of a sensory system may serve singular functions. For example, the *Limulus* brain segregates the processing of visual information, devoting a major locus in the medulla to the region of the visual field that views potential mates. Horizontal strips of ommatidia serving this region form a precise map onto an expanded locus in the medulla (Chamberlain and Barlow, 1982), suggesting that the primary task of this region is mate detection (Dodge *et al.*, 1999). Understanding the functions of such specialized regions of a sensory system and the underlying neural integrative mechanisms may aid in the design of artificial sensory systems useful for remote sensing and robotics.

Excitation and inhibition are universal mechanisms for processing the spatial and temporal features of sensory information. They "tune" sensory systems, selecting essential features from a world rich in information. Remarkably,

the integrative mechanisms of the *Limulus* eye make it highly sensitive to moving, mate-like objects. Mechanisms of adaptation enable the eye to operate over wide ranges of environmental conditions. In sum, the neural mechanisms of this so-called "primitive" eye encode and analyze visual information and send a highly processed neural image to the brain both day and night.

The implications for artificial sensory systems are (1) a relatively simple neural circuit can encode and process sensory information, and (2) the same neural circuit can operate over a wide range of environmental conditions. Can an artificial system be designed and constructed with these properties? We implemented a software-based computational model that incorporates these properties, but with current hardware it cannot function in real time. Computations are an order of magnitude slower than real time; that is, computing the eye's response (neural images) to 6 s of visual input requires about 60 s. At this time a computational model appears unrealistic. An alternative approach is to construct a silicon retina having all the known properties of the *Limulus* eye. Such artificial retinas have been fabricated (Mahowald and Mead, 1991), but they are mostly hardwired and not readily adaptable to changing environmental conditions. However, techniques of microcircuitry are advancing at a rapid pace. Perhaps in the not-too-distant future it will be possible to fabricate a silicon retina with stimulus-dependent circuitry that can simulate an eye's numerous adaptative mechanisms. Such a dynamic "softwired eye" would find many uses, from remote sensing in hazardous environments to the navigational control of robots. Because *Limulus* incorporates many of the integrative mechanisms found in more complex vertebrate eyes, it is conceivable that a *Limulus*-inspired "softwired eye" may also prove useful as the first stage of a prosthetic visual system for humans.

Acknowledgments

Literature Cited

Alonso, J-M., W. M. Usrey, and R. C. Reid. 1996. Precisely correlated firing in cells of the lateral geniculate nucleus. *Nature* **383:** 815–819.

Barlow, R. B. 1969. Inhibitory fields in the *Limulus* lateral eye. *J. Gen. Physiol.* **54:** 383–396.

Barlow, R. B., and D. A. Quarles. 1975. Mach bands in the lateral eye of *Limulus:* Comparison of theory and experiment. *J. Gen. Physiol.* **65:** 709–730.

Barlow, R. B., S. J. Bolanowski, and M. L. Brachman. 1977. Efferent optic nerve fibers mediate circadian rhythms in the *Limulus* eye. *Science* **197:** 86–89.

Barlow, R. B., S. C. Chamberlain, and J. Z. Levinson. 1980. The *Limulus* brain modulates the structure and function of the lateral eye. *Science* **210:** 1037–1039.

Barlow, R. B., R. R. Birge, E. Kaplan, and J. R. Tallent. 1993a. On the molecular origin of photoreceptor noise, retinas. *Nature* **366:** 64–66.

Barlow, R. B., R. Prakash, and E. Solessio. 1993b. The neural network of the *Limulus* retina: From computer to behavior. *Am. Zool.* **33:** 66–78.

Barlow, R. B., Jr. 1983. Circadian rhythms in the *Limulus* visual system. *J. Neurosci.* **3:** 856–870.

Barlow, R. B., Jr., and S. C. Chamberlain. 1980. Light and circadian clock modulate structure and function in *Limulus* photoreceptors. Pp. 247–269 in *The Effects of Constant Light on Visual Processes,* T. P. Williams and B. N. Baker, eds. Plenum Press, New York.

Barlow, R. B., Jr., L. C. Ireland, and L. Kass. 1982. Vision has a role in *Limulus* mating behavior. *Nature* **296:** 65–66.

Barlow, R. B., Jr., E. Kaplan, G. H. Renninger, and T. Saito. 1987. Circadian rhythms in *Limulus* photoreceptors. 1. Intracellular recordings. *J. Gen. Physiol.* **89:** 353–378.

Barlow, R. B., Jr., S. C. Chamberlain, and H. K. Lehman. 1989. Circadian rhythms in invertebrate vision. Pp. 257–280 in *Facets of Vision,* D. C. Stavenga and R. C. Hardie, eds. Springer-Verlag, Berlin.

Batra, R., and R. B. Barlow, Jr. 1990. Circadian rhythms in the temporal response of the *Limulus* lateral eye. *J. Gen. Physiol.* **95:** 229–244.

Battelle, B. A., C. D. Williams, J. L. Schremser-Berlin, and C. Cacciatore. 2000. Regulation of arrestin mRNA levels in *Limulus* lateral eye: Separate and combined influences of circadian efferent input and light. *Visual Neurosci.* **17:** 217–227.

Berry, M. J., D. K. Warland, and M. Meister. 1997. The structure and precision of retinal spike trains. *Proc. Natl. Acad. Sci. USA* **94:** 5411–5416.

Brenner, N., W. Bialek, and R. R. de Ruyter van Steveninck. 2000. Adaptive rescaling maximizes information transmission. *Neuron* **26:** 695–702.

Brivanlou, I. H., D. K. Warland, and M. Meister. 1998. Mechanisms of concerted firing among retinal ganglion cells. *Neuron* **20:** 527–539.

Chamberlain, S. C., and R. B. Barlow, Jr. 1977. Morphological correlates of efferent circadian activity and light adaptation in the *Limulus* lateral eye. *Biol. Bull.* **153:** 418–419.

Chamberlain, S. C., and R. B. Barlow, Jr. 1979. Light and efferent activity control rhabdom turnover in *Limulus* photoreceptors. *Science* **206:** 361–363.

Chamberlain, S. C., and R. B. Barlow, Jr. 1982. Retinotopic organization of lateral eye input to the *Limulus* brain. *J. Neurophysiol.* **48:** 505–520.

Chamberlain, S. C., and R. B. Barlow, Jr. 1984. Transient membrane shedding in *Limulus* photoreceptors: Control mechanisms under natural lighting. *J. Neurosci.* **4:** 2792–2810.

Chamberlain, S. C., and R. B. Barlow, Jr. 1987. Controls of structural rhythms in the lateral eye of *Limulus:* Interactions of diurnal lighting and circadian efferent activity. *J. Neurosci.* **7:** 2135–2144.

DeVries, S. H. 1999. Correlated firing in rabbit retinal ganglion cells. *J. Neurophysiol.* **81:** 908–920.

Dodge, F. A., J. M. Hitt, and R. B. Barlow. 1999. Segregation of visual information processing in the *Limulus* brain. *Soc. Neurosci. Abstr.* **25:** 1429.

Dowling, J. E. 1987. *The Retina: An Approachable Part of the Brain.* Harvard University Press, Cambridge, MA.

Field, D. 1994. What is the goal of sensory coding? *Neural Comput.* **6:** 559–601.

Harris, R. A., D. C. O'Carroll, and S. B. Laughlin. 2000. Contrast gain reduction in fly motion adaptation. *Neuron* **28:** 595–606.

Hartline, H. K., and F. Ratliff. 1957. Inhibitory interactions of receptor units in the eye of *Limulus. J. Gen. Physiol.* **40:** 357–376.

Hartline, H. K., and F. Ratliff. 1958. Spatial summation of inhibitory

influences in the eye of *Limulus,* and the mutual interactions of receptor units. *J. Gen. Physiol.* **41**: 1049–1066.

Herzog, E. H., M. K. Powers, and R. B. Barlow. 1996. *Limulus* vision in the ocean day and night: Effects of image size and contrast. *Visual Neurosci.* **13**: 31–41.

Hitt, J. M., V. Ruta, F. A. Dodge, and R. B. Barlow. 2000. Explaining night vision in *Limulus. Invest. Ophthalmol. Visual Sci.* **41**: S28.

Kaplan, E., and R. B. Barlow, Jr. 1980. Circadian clock in *Limulus* brain increases response and decreases noise of retinal photoreceptors. *Nature* **286**: 393–395.

Kaplan, E., R. B. Barlow, G. Renninger, and K. Purpura. 1990. Circadian rhythms in *Limulus* photoreceptors. II. Quantum bumps. *J. Gen. Physiol.* **96**: 665–685.

Kass, L., and M. Berent. 1988. Circadian rhythms in adaptation to light of *Limulus* photoreception. *Comp. Biochem. Physiol.* **91**: 229–239.

Krutky, M. A., J. L. Atherton, S. Smith, F. A. Dodge, and R. B. Barlow. 2000. Do the properties of underwater lighting influence the visually guided behavior of *Limulus? Biol. Bull.* **199**: 178–179.

Laughlin, S. B. 1994. Matching coding, circuits, cells, and molecules to signals: General principles of retinal design in the fly's eye. *Prog. Ret. Eye Res.* **13**: 165–196.

Lettvin, Y. L., H. R. Maturana, W. S. McColluch, and W. H. Pitts. 1959. What the frog's eye tells the frog's brain. *Proc. Inst. Radio Eng.* **47**: 1940–1951.

Mahowald, M. A., and C. Mead. 1991. The silicon retina. *Sci. Am.* **264**: 76–82.

Meister, M., and M. J. Berry, II. 1999. The neural code of the retina. *Neuron* **22**: 435–450.

Meister, M., J. Pine, and D. A. Baylor. 1994. Multi-neuronal signals from the retina: Acquisition and analysis. *J. Neurosci. Methods* **51**: 95–106.

Passaglia, C. L., F. A. Dodge, E. H. Herzog, S. Jackson, and R. B. Barlow. 1997a. Deciphering a neural code for vision. *Proc. Natl. Acad. Sci. USA* **94**: 12649–12654.

Passaglia, C. L., M. E. McSweeney, K. M. Stewart, E. Kim, E. J. Mole, M. K. Powers, and R. B. Barlow. 1997b. Visual performance of horseshoe crabs: Role of underwater lighting. *Biol. Bull.* **193**: 205–207.

Passaglia, C. L., F. A. Dodge, and R. B. Barlow. 1998. A cell-based model of the *Limulus* lateral eye. *J. Neurophysiol.* **80**: 1800–1815.

Powers, M. K., and R. B. Barlow, Jr. 1985. Behavioral correlates of circadian rhythms in the *Limulus* visual system. *Biol. Bull.* **169**: 578–591.

Powers, M. K., R. B. Barlow, and L. Kass. 1991. Visual performance of horseshoe crabs day and night. *Visual Neurosci.* **7**: 179–189.

Ratliff, F. 1974. Studies of excitation and inhibition in the retina. Rockefeller University Press, New York.

Renninger, G. H., and R. B. Barlow, Jr. 1979. Lateral inhibition, excitation, and the circadian rhythm of the *Limulus* compound eye. *Soc. Neurosci. Abstr.* **5**: 804.

Renninger, G. H., E. Kaplan, and R. B. Barlow, Jr. 1984. A circadian clock increases the gain of photoreceptor cells of the *Limulus* lateral eye. *Biol. Bull.* **167**: 532.

Rieke, F., D. Warland, R. R. DeRuyter van Steveninck, and W. Bialek. 1997. *Spikes: Exploring the Neural Code.* MIT Press, Cambridge, MA.

Ruta, V. J., F. A. Dodge, and R. B. Barlow. 1999. Evaluation of circadian rhythms in the *Limulus* eye. *Biol. Bull.* **197**: 233–234.

Teeters, J., A. Jacobs, and F. Werblin. 1997. How neural interactions form neural responses in the salamander retina. *J. Comp. Neurosci.* **4**: 5–27.

Warland, D. K., P. Reinagel, and M. Meister. 1997. Decoding visual information from a population of retinal ganglion cells. *J. Neurophysiol.* **78**: 2336–2350.

Warzecha, A. K., and M. Egelhaaf. 1997. How reliably does a neuron in the visual motion pathway of the fly encode behaviourally relevant information? *Eur. J. Neurosci.* **9**: 1365–1374.

Werblin, F. S. 1991. Synaptic connections, receptive fields, and patterns of activity in the tiger salamander retina. *Invest. Ophthalmol. Visual Sci.* **32**: 459–483.

Wong, R. O., A. Chernjavsky, S. J. Smith, and C. J. Shatz. 1995. Early functional networks in the developing retina. *Nature* **374**: 716–718.